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Hydrodynamic mediation of density-dependent growth and adult–juvenile interactions of a spionid polychaete

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Abstract

We performed an experiment to test the effects of adult density on the growth rates of juvenile *Polydora cornuta*. Our experiment was performed in three identical counter-rotating annular flumes, each set to one of three different flow speeds for a period of 3 d (U_{5mm} = 3, 6, or 12 cm s^{-1}, where U_{5mm} = velocity measured 5 mm above bottom). We implanted replicate vials containing a premeasured juvenile *P. cornuta* and either 0, 2, or 5 adults into a 2-cm layer of sediment in the flume. The relative growth rates of the juveniles were determined by measuring each juvenile's body volume before and after the 3-d deployment in the flumes. We repeated the experiment three times. The growth rates of juveniles were negatively affected by adult density at the two slower flows, but there was no evidence of negative density-dependent growth at the fastest flow. In the two slower flows, the mean relative growth rate of juveniles declined from 53 to 34% d^{-1} as the number of adults increased from 0 to 5. Fecal mounds accumulated near adults in the two slower flows, but mounds were absent in the fastest flow. The hydrodynamic mediation of the effects of density suggests that the strength of density-dependent and adult–juvenile interactions in nature are likely to be mediated by flow. Spionids should be able to achieve higher population densities at places where or times when faster flows facilitate suspension feeding and reduce the effects of biogenic disturbance of the sediment–water interface.

Flow in the benthic boundary layer above soft sediments influences infauna in many ways, including effects on dispersal (e.g., Powers and Peterson 2000; Stocks 2002), larval settlement and recruitment (e.g., Snelgrove and Butman 1994; Fingerut et al. 2003), feeding behaviors and mechanics (e.g., Shimeta and Jumars 1991; Miller et al. 1992), and the growth of individual organisms (e.g., Judge et al. 1992; Lenihan et al. 1996). Virtually all of these processes are also affected by density-dependent interactions among individuals within a population or community (e.g., Peterson and Black 1987; Wilson 1991). Interactions between flow and the density and diversity of passive suspension feeders have been shown to enhance ecosystem functioning (Cardinale et al. 2002). Relative to studies of flow-mediated competition and gregarious larval settlement in hard-substrate systems (e.g., Pawlik et al. 1991; Genin et al. 1994; Fonseca and Hart 1996), few researchers have tested the interactions between hydrodynamic conditions and the density dependence of key ecological processes in soft sediments (e.g., Olafsson 1986; Powers and Peterson 2000).

We performed a controlled experiment in laboratory flumes to test the effects of adult density on the growth rates of conspecific juveniles of a common spionid polychaete, *Polydora cornuta*. Most spionids are interface feeders (Dauer et al. 1981), switching between deposit feeding in slow flows and suspension feeding in faster flows that have higher fluxes of suspended food (Taghon and Greene 1992; Bock and Miller 1996). The growth of *P. cornuta* is greatly enhanced by increasing flow and the flux of suspended food; the relative growth rate of isolated juveniles can be as high as 60% d^{-1} under certain flow conditions (Hentschel 2004; Hentschel and Larson 2005). Spionid populations often achieve densities over 10,000 m^{-2} (e.g., Levin 1981; Zajac 1991). The activities of spionids, especially feeding and tube building, have significant impacts on other members of soft-sediment communities (e.g., Cummings et al. 1996; Bolam and Fernandes 2003).

Taghon (1992) performed the only previous flume experiments designed to test the effects of density on the growth rates of spionids. Contrary to expectations, Taghon's (1992) experiments on medium-sized juveniles of *Pseudopolydora kempi japonica* and *Boccardia pugettensis* did not reveal effects of intraspecific density on growth rates, even when the densities were 940% and 220% of the in situ densities of *Pseudopolydora* and *Boccardia*, respectively. Taghon (1992) did, however, measure density-dependent emigration and found that deposit-feeding individuals had a greater spacing between neighbors than did suspension-feeding individuals. The movement and spacing of individuals might have reduced the effects of density on worms' growth rates. Several aspects of the experimental design suggest that these initial results might be difficult to extrapolate beyond the conditions in Taghon's (1992) flume. The experiments included just two flow regimes: (1) a slow flow of ~2 cm s^{-1} with a brief, pulsed increase every 3 h to transport sediment as bedload to deposit-feeding worms and (2) a constant flow of ~6 cm s^{-1} in which unfiltered seawater was supplied as suspended food (Taghon 1992). Taghon and Greene (1992) discuss how the supply of suspended particles pumped through this flume might have limited worms' growth.

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Our experiment in replicate flumes set to three different flow speeds measured the growth rates of small, recently settled juvenile *P. cornuta* that were surrounded by varying numbers of much larger adults. We controlled the quantity and quality of suspended and deposited food and tested two main hypotheses: (1) the growth rates of juveniles vary with adult density and (2) the effect of adult density on juvenile growth varies among flow speeds.

Methods

General procedures for collecting live *P. cornuta*, measuring their body sizes, and transplanting worms into the counter-rotating annular flumes are described in detail in Hentschel (2004). *Polydora cornuta* were collected from an intertidal sandflat at Shark River Island, New Jersey. Prior to each experiment, sorted worms were anesthetized in 3% $MgCl_2$ and divided into two length classes: 1–4 mm and 9–15 mm. This species becomes sexually mature at a body length of ~1 cm (Hentschel 1998, 2004), and we refer to the two length classes as juveniles and adults.

Size measurements were made of all juveniles by video microscopy and image analysis (Hentschel 2004). We measured each individual's total body length and body width at 5 locations between the anterior and posterior end. Length and width measurements were used to calculate each individual's body volume at the start of an experiment, modeling the worm as a series of four conical frustums. The volume of each frustum is calculated as

$$V = (\pi/3)\cdot L\cdot[(W_1/2)^2 + (W_1/2)(W_2/2) + (W_2/2)^2] \quad (1)$$

where V is the volume of the frustum, L is the length of the frustum, and W_1 and W_2 are the two width measurements at each end of the frustum. The entire body volume of a worm is calculated by summing the volumes of the four conical frustums (Hentschel 2004).

After a juvenile was measured, it was transferred from 3% $MgCl_2$ to filtered seawater and then placed in a numbered vial containing sediment. The sediment had been collected from the field site, frozen and thawed, sieved to remove particles greater than 0.3 mm, and frozen and thawed again before adding it to vials. The vials were a series of concentric cylinders (all 2.0 cm high) made from plastic syringes and pipet tips with Hot Melt Glue sealing the bottom. After filling a vial with sediment, a premeasured juvenile was pipetted into the central cylinder (0.6 cm diameter). Juveniles typically built a sediment tube inside the central cylinder within 1 h (vials were examined at 6× magnification to confirm the presence of a tube-dwelling juvenile). A controlled number of adults (0, 2, or 5) was then placed between the central cylinder and the middle cylinder (1.4 cm diameter). We randomly assigned at least 30 premeasured juveniles to each adult-density treatment. The surface area of the middle cylinder, which contained the juvenile and adult worms, was 1.54 cm^2. Vials were left undisturbed for 1–2 h to allow adults to build tubes. An outer cylinder (2.5 cm diameter) surrounded both of the smaller cylinders and facilitated the transfer of the controlled-density vials. Because we had a limited number of these vials and wanted large sample sizes, we also used a simpler vial for many of the solitary juveniles (a single cylinder 1.4 cm diameter × 2.0 cm high). A pilot study showed no significant difference between the growth rates of solitary juveniles residing in either type of vial, and we confirmed this during the present flume experiments (following).

After worms built tubes, the vials were placed in holes drilled in 1.3-cm-thick polyvinyl chloride (PVC) slabs (~15 × 30 cm). Each PVC slab contained 8–12 vials that were separated by at least 2.5 cm. Locations of individual vials within and among slabs were random. Slabs containing vials were then placed in a seawater table (15°C, salinity = 30). All worms for a single experiment were measured, implanted in vials, and placed in the seawater table during a single 12-h period. Worms acclimated to vials overnight in the seawater table for an additional 15–18 h prior to being implanted in flumes.

The following day, PVC slabs containing vials were implanted into a 2-cm-deep layer of silica sand (~0.75 mm diameter) in the bottom of a flume. PVC slabs were planted in a single section of the flume, roughly one eighth of the channel's circumference. Vials occupied the center 10 cm of the channel. The sand layer in the entire flume was smoothed to a height of 2 cm so the top edges of the vials were flush with the sand–water interface.

After vials were implanted in the sand, the flume was filled with 5-μm-filtered seawater to achieve a 28-cm-deep water column. A thin layer (~2 mm thick) of field-collected sediment was then deposited above the sand layer and the vials within it by creating a slurry and allowing the sediment to settle in the flume overnight (Hentschel 2004). Flow treatments began the next morning, 15–18 h after the field-collected sediment was added.

We planted PVC slabs containing worms into three identical counter-rotating annular flumes (Hentschel 2004; Hunt 2004). PVC slabs containing vials were randomly assigned to flumes. Each flume initially contained at least nine replicate vials of each of the three density treatments (0, 2, or 5 adults per vial) and was set to one of three constant, unidirectional flow speeds: U_{5mm} = 3, 6, or 12 cm s^{-1}, where U_{5mm} denotes the mean horizontal velocity measured with a laser-Doppler velocimeter positioned 0.5 cm above the sediment–water interface. The flow-speed assignments among the three flumes were made randomly. The fastest flow (U_{5mm} = 12 cm s^{-1}) was slower than the critical erosion velocity of the sediment in the smooth bed (Hentschel 2004). Any structure that extends higher in the benthic boundary layer will experience faster velocities and likely be eroded. Hentschel (2004) reports flume-rotation settings for the three flow treatments. Shear velocities (U_*) for the three flows were 0.1, 0.4, and 0.7 cm s^{-1} (Hentschel 2004). We ran the three flumes simultaneously at 20°C for 3 d.

To provide and control suspended food, a nonliving algal slurry (C-6 Slurry, Coast Seafoods) was added to each flume each day during a 3-d experiment. Hentschel and Larson (2005) compared the growth rates of solitary *P. cornuta* and *Streblospio benedicti* in flumes containing two different concentrations of this algal slurry. Our adult-density experiments were run at the high food concentration of Hentschel and Larson (2005). The mean concentration of suspended particulate N in the flumes was 0.26 mg L^{-1} during our ex-

periments, which is similar to concentrations in the field (mean = 0.34; Hentschel 2004).

At the end of a 3-d run, the PVC slabs and the worm vials were recovered from the three flumes (Hentschel 2004). Each recovered juvenile was remeasured to calculate its body volume at the end of its 3-d run. Relative growth rates (RGR) were calculated as

$$RGR = [\ln(V_f) - \ln(V_i)]/time \quad (2)$$

where V_f and V_i are measurements of each individual's final and initial body volume, respectively (Hentschel 2004). The initial sizes of juveniles and adults were different enough that, during the 3-d experiment, juveniles could not grow as large as the initial size of adults. This facilitated the unambiguous identification of the premeasured juvenile in each vial. In addition to recovering and remeasuring juveniles, we also enumerated the adults recovered from each vial. We had anticipated some adult emigration during the 3-d experiment and decided a priori that any of the vials initially established with five adults would be analyzed as replicates in the five-adult treatment if at least four adults were recovered. In the end, this a priori decision had little effect on our analysis; only 2% of the five-adult vials had a missing adult.

The 3-d flume experiment was repeated three times: 10 July 2000–13 July 2000, 21 July 2000–24 July 2000, and 7 September 2000–10 September 2000. In the first trial, the flume set to U_{5mm} = 12 cm s^{-1} included nine solitary juveniles in the concentric vials and five solitary juveniles in the simple vials so we could confirm that the growth of solitary juveniles was not significantly affected by the type of vial. In the second trial, the flume set to U_{5mm} = 3 cm s^{-1} included 9 solitary juveniles in the concentric vials and 10 solitary juveniles in the simple vials. In the third trial, the flume set to U_{5mm} = 6 cm s^{-1} included eight solitary juveniles in the concentric vials and five solitary juveniles in the simple vials.

Because our main focus was to test the effect of adult density on the growth of juveniles at each flow speed, we planned a priori to analyze the effect of adult density within each flume separately. We performed two analyses of the density effect in each flume: a one-way analysis of variance (ANOVA) and *t*-test comparisons between the adult-density treatments. Both tests were planned a priori. To test for an interaction between the effects of flow speed and adult density, we combined the three trials and performed a two-way ANOVA (flow speed, adult density) on the mean juvenile growth rates for each density treatment within each flume. This analysis of means avoids pseudoreplication of nonindependent juveniles in a given density treatment in a given flume (Hurlbert 1984).

Results

Overall, we recovered 88% of the premeasured juveniles, and there was no evidence of a relationship between recovery success and adult density. In fact, we recovered all 34 juveniles and all 70 adults that were implanted in the flume set to U_{5mm} = 6 cm s^{-1} during the first trial.

None of the three comparisons between solitary juveniles in the two types of vials revealed significant differences in juvenile growth (*t*-tests, $p > 0.18$; Fig. 1). Consequently, we pooled both types of zero-adult vials when analyzing the effects of adult density on juvenile growth. This resulted in the zero-adult treatment having 13–19 replicates in some flumes (Fig. 1).

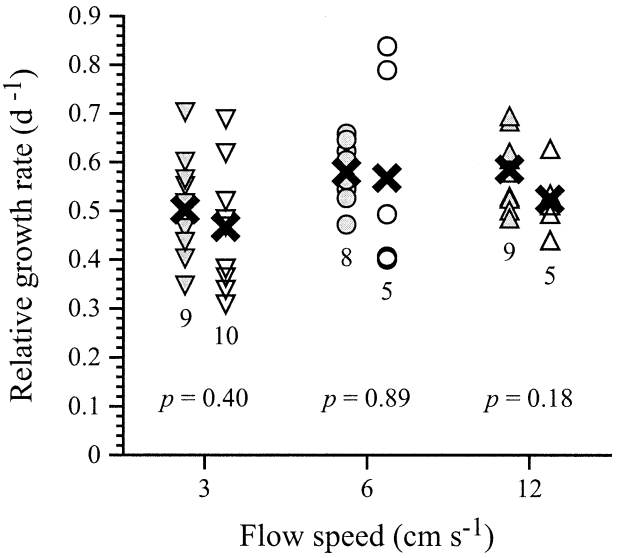

Fig. 1. Comparison between the relative growth rates (RGR) of solitary juveniles placed in concentric-cylinder vials versus a simple vial (1.4 cm diameter). Each gray-filled symbol is the RGR of an individual juvenile in a concentric-cylinder vial. Open symbols represent juveniles in simple vials. The mean RGR within each vial type is indicated by a black X. Sample sizes are listed below each group. *p* values indicate results of *t*-tests comparing RGRs between the two vial types. Comparisons were made at a different flow speed (U_{5mm}) during each of the three trials (U_{5mm} = 3 cm s^{-1} during 21 July–24 July, U_{5mm} = 6 cm s^{-1} during 7 September–10 September, and U_{5mm} = 12 cm s^{-1} during 10 July–13 July).

The three trials consistently showed that increasing numbers of adults negatively affected the growth rates of juvenile *P. cornuta* at the two slowest flow speeds, but none of the flumes set to U_{5mm} = 12 cm s^{-1} revealed negative density-dependent growth (Fig. 2). At U_{5mm} = 3 cm s^{-1}, both the first and second trials showed a significant decline in juvenile growth rate as adult density increased ($F_{2,25} = 9.978$, $p < 0.001$ and $F_{2,32} = 11.891$, $p < 0.001$, respectively); the third trial showed a similar trend (Fig.2A), but it was not significant at $\alpha = 0.05$ ($F_{2,24} = 2.867$, $p = 0.076$). All three flumes set to U_{5mm} = 6 cm s^{-1} showed a significant decline in juvenile growth as adult density increased ($F_{2,31} = 12.574$, $p < 0.001$; $F_{2,24} = 6.213$, $p = 0.007$; and $F_{2,27} = 4.878$, $p = 0.032$ for the first, second, and third trials, respectively). In most of the flumes set to U_{5mm} = 3 or 6 cm s^{-1}, *t*-tests revealed significant differences between the growth rates of juveniles in the two-adult treatment and either extreme of zero or five adults. For example, in the flume set to U_{5mm} = 6 cm s^{-1} in the first trial (Fig. 2B), the zero- and two-adult treatments differed ($p = 0.028$) and so did the two- and five-adult treatments ($p = 0.033$). The flumes set to U_{5mm} = 12 cm s^{-1} in the second and third trials did not show a significant effect of adult density on the growth rate of juveniles ($F_{2,26} = 0.096$, $p = 0.909$; $F_{2,20} = 2.708$, $p = 0.091$, respec-

tively). Surprisingly, the flume set to U_{5mm} = 12 cm s^{-1} in the first trial showed a significant, positive effect of adult density ($F_{2,29}$ = 4.459, p = 0.020); *t*-tests showed that juveniles in the two-adult vials grew significantly faster than solitary juveniles in this flume (Fig. 2C; $p < 0.001$).

The significant interaction between the effects of flow speed and adult density was confirmed by the two-way ANOVA ($F_{4,18}$ = 2.987, p = 0.047). This analysis of the treatment means from all three trials also confirmed the overall effects of adult density ($F_{2,18}$ = 6.419, p = 0.008) and flow speed ($F_{2,18}$ = 14.501, $p < 0.001$).

During the 3-d experiments, we also observed the accumulation of prominent fecal mounds (~2 cm high × 3 cm diameter) in all flumes set to U_{5mm} = 3 or 6 cm s^{-1}. Fecal mounds above vials containing five adults were noticeably larger and formed more quickly than those above vials containing two adults (Fig. 3A). These mounds did not form in any of the flumes set to U_{5mm} = 12 cm s^{-1} (Fig. 3B), most likely because feces were continuously eroded in this flow rather than accumulating as mounds. In the flumes set to U_{5mm} = 3 or 6 cm s^{-1}, adults typically extended their U-shaped tubes several mm above the sediment–water interface (Fig. 3A). We never observed distinct tubes above the sediment–water interface in any of the flumes set to U_{5mm} = 12 cm s^{-1} (Fig. 3B).

Discussion

In contrast with Taghon (1992), we found clear evidence that adult density negatively affected the growth of conspecific juvenile spionids. The three densities in our 1.54 cm^2 vials (0.65, 1.95, and 3.90 worms cm^{-2}) were within the range of natural population densities reported for *P. cornuta* (Zajac 1991) and similar spionids (e.g., Levin 1981). Most important, we found that the effects of adult density depended strongly on hydrodynamic conditions; the presence of adults slowed the growth of juveniles at the two slow flow speeds but not at the fastest flow we tested.

Our experiment on *P. cornuta* was designed very differently than Taghon's (1992) experiments on *Pseudopolydora kempi japonica* and *Boccardia pugettensis.* Rather than estimating the growth of several medium-sized worms placed in a single bottle (Taghon 1992), we measured the growth rates of very small juveniles that were surrounded by much larger adults. Having only one juvenile per vial ensured that the measurements of body sizes at the start and end of the experiment were made on the same individuals. We also expect the difference in size between adults and juveniles magnified the effects of density relative to those that would occur when similarly sized individuals interact. Furthermore, our concentric vials constrained the movement of the targeted juveniles; they could not escape the impact of adults by altering the spacing among neighbors, as observed by Taghon (1992). To avoid complications associated with natural seston (Taghon 1992; Taghon and Greene 1992), we tightly controlled the suspended food by adding known amounts of microalgae and monitoring concentrations in the flumes each day (Hentschel and Larson 2005). The mean growth rates we measured for solitary *P. cornuta* (30–60% d^{-1}) were much faster than those Taghon (1992) measured for solitary *P. kempi japonica* and *B. pugettensis* (*also see* Taghon and Greene 1992; Hentschel and Larson 2005). The rapid growth of solitary juveniles probably facilitated our detection of a

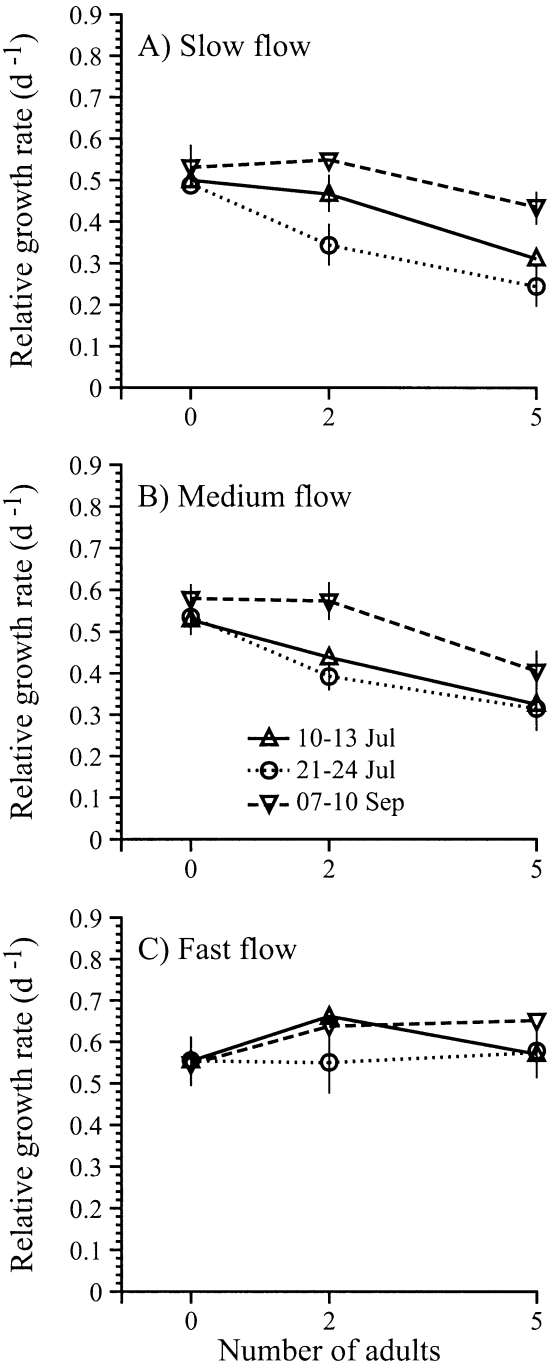

Fig. 2. Relative growth rates (RGR) of juvenile *Polydora cornuta* versus the number of adults. Plotted symbols represent the mean RGRs (±SE) for each of the three adult-density treatments in a single flume. Data from the three trials are distinguished by different symbols and line patterns (B). In most cases, error bars are smaller than the plotted symbol. Data from the flumes set to U_{5mm} = 3 cm s^{-1}, U_{5mm} = 6 cm s^{-1}, and U_{5mm} = 12 cm s^{-1} are plotted in A, B, and C, respectively.

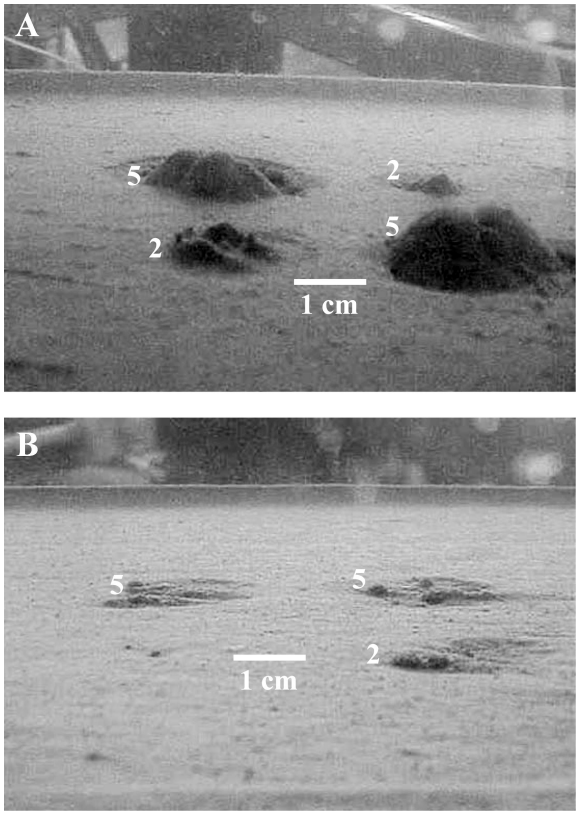

Fig. 3. Photographs of fecal mounds typically (A) present or (B) absent at the end of a 3-d flume experiment. (A) A flume set to U_{5mm} = 6 cm s^{-1} shows the fecal mounds produced above five-adult and two-adult treatments (flumes set to U_{5mm} = 3 cm s^{-1} had similar mounds). U-shaped tubes constructed by the two adults in the lower left are visible. (B) A flume set to U_{5mm} = 12 cm s^{-1} shows much less biogenic disturbance, including an absence of tubes above the sediment–water interface.

density-dependent reduction on the order of 15–20% d^{-1} by increasing the ratio of signal to statistical noise. Most important, we performed our manipulation of adult density at three different flow speeds by using three identical flumes run simultaneously.

There are many possible interactions between adult and juvenile spionids that might reduce juvenile growth. For example, Levin (1981) observed aggressive palp interactions that can disrupt feeding activity. The mere presence of a suspension-feeding neighbor upstream can alter velocities and turbulence on a local scale (e.g., Johnson 1990; Sebens et al. 1997; Thompson et al. 2004).

Our growth-rate experiment was not designed to identify the mechanism(s) that caused juvenile growth to decline in the presence of adults, but we did observe that the accumulation of fecal mounds correlated with the interaction between the effects of flow and adult density. We suspect, therefore, that the accumulation of feces in the two slowest flow speeds was at least one cause of the density-dependent decline in juvenile growth. Adult defecation probably forced juveniles to spend time and energy extending their tubes to avoid burial and also might have interfered directly with juveniles' feeding. The current in the flumes set to U_{5mm} = 12 cm s^{-1} seems to have been fast enough to prevent the formation of fecal mounds and provides the most likely explanation for the absence of negative density-dependent effects in the fastest flow we tested.

Although the presence of fecal mounds corresponded with reduced growth rates, we did not find any evidence that the mounds produced by adults affected the survival of juveniles during our 3-d experiments (i.e., 88% of the juveniles were recovered alive). Larger mounds produced by arenicolid polychaetes and thalassinid shrimps can affect the survival of juvenile spionids (Wilson 1991). Lindsay et al. (1996) simulated the spatial and temporal heterogeneity of predation and fecal-mound disturbance in soft sediments and assumed that juveniles buried by arenicolid feces suffered 100% mortality. Our data suggest such an assumption overemphasizes the short-term effects of fecal mounds and other small-scale depositional disturbances, especially when flow is fast enough to prevent the accumulation of recent deposits above the sediment–water interface. Whether flume experiments lasting longer than 3 d would reveal negative effects of adult density on juvenile survival remains an open question, but the fact that juveniles in our slow-flow, five-adult treatments were able to increase their body volumes at rates over 25% d^{-1} in the short term should quickly reduce the disparity in size between juveniles and adults that interact for extended periods.

Our experiment focused on the density of a single species; other species might show different trends and interspecific interactions might differ from intraspecific ones and vary with flow. For example, Taghon (1992) found that the density of *B. pugettensis* had a negative effect on the growth of *P. kempi japonica* when slow flow limited worms to deposit feeding. Experiments on solitary individuals of *Streblospio benedicti* suggest that the growth rate of this species depends much less on flow than does the growth of *P. cornuta* (Hentschel and Larson 2005), and we suspect that *S. benedicti* might show greater effects of density relative to those we measured for *P. cornuta.* More broadly, Cardinale et al. (2002) showed that species diversity can lead to hydrodynamic facilitation; feeding rates of caddisfly larvae were affected by the shading of flow downstream from neighbors to a greater extent in monocultures than in a three-species assemblage.

We manipulated density on a small spatial scale. A dense assemblage covering a larger area might cause skimming flow (e.g., Eckman et al. 1981; Friedrichs et al. 2000). In general, the wakes created by individuals are likely to interact when the density of roughness elements (e.g., worm tubes) exceeds 8.3% of the bed area (Eckman et al. 1981; Friedrichs et al. 2000). U-shaped tubes of adult *P. cornuta* measure ~1–2 mm diameter. For a 2-mm tube, the roughness density will equal 8.3% at a density of 26,500 m^{-2}. This density is in the range reported for *P. cornuta* (Zajac 1991) and similar spionids (e.g., Levin 1981), suggesting that skimming flow should be considered when studying density-dependent interactions in large patches. We note, however, that the height of tubes can vary (e.g., Muschenheim 1987), and we did not observe tubes in the fastest flow we tested (Fig. 3). Predicting the effects of various densities and patch sizes on downstream velocities, turbulence, and

particle fluxes will require detailed measurements of velocities and particle concentrations on small scales near individual worms in dense patches (Shimeta and Jumars 1991).

In addition to spatial variability, hydrodynamic conditions in nature also vary on a range of temporal scales. Like most flume experiments, the three constant, unidirectional flows in our experiments were simplified relative to conditions that are likely to influence density-dependent and juvenile–adult interactions in situ. For example, fecal mounds usually are eroded during inundation of an intertidal site. Tidal currents also vary during the monthly lunar cycle. Larvae recruiting to areas of high population density will probably be able to grow more rapidly as juveniles if they settle a few days before the maximal tidal exchange during a spring tide rather than a few days before a neap tide. Similarly, larvae settling prior to a few days of storm activity will probably suspension feed more frequently (Bock and Miller 1995) and grow more rapidly than will juveniles that settle a few days before calm weather. Several studies have pointed to the early juvenile period as a possible bottleneck in the dynamics of benthic populations (e.g., Olafsson et al. 1994; Hentschel 1998); even a few days of favorable flow might reduce density-dependent, competitive interactions and ease the transition from pelagic larva to benthic juvenile. Ultimately, in-situ manipulations of flow (e.g., Judge et al. 1992; Powers and Peterson 2000) and laboratory simulations of flow variability on a variety of temporal scales will be required to test the effects of various hydrodynamic conditions on the density-dependent growth rates of infauna.

The hydrodynamic mediation of density-dependent growth and juvenile–adult interactions has several implications for the dynamics of spionid populations and the communities in which they often are important members (e.g., Cummings et al. 1996; Stehlik and Meise 2000; Bolam and Fernandes 2003). Several models of spionid populations point to juvenile growth rate as a central parameter (e.g., Levin and Huggett 1990; Zajac 1991). Because these models were based, in part, on rates of juvenile growth measured in still-water lab experiments, the number of individuals in a population is likely to increase much more rapidly in nature, where some flow and flux of seston always occurs. Faster flows probably will facilitate higher population densities. Dense patches of spionids can have a variety of community-level effects, including the exclusion of species (Bolam and Fernandes 2003). Spionids also are common items in the diets of fishes and shorebirds (e.g., Zajac 1995; West et al. 2003); this food resource for higher trophic levels will be enhanced when or where hydrodynamic conditions favor the suspension feeding of spionids in high densities.

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